

ABSTRACT

Title of Document: PATTERNS OF HOST USE BY BROWN
MARMORATED STINK BUG,
HALYOMORPHA HALYS (HEMIPTERA:
PENTATOMIDAE), IN WOODY
ORNAMENTAL TREES AND SHRUBS

Erik John Bergmann, Master of Science, 2015

Directed By: Professor Michael Joseph Raupp
Department of Entomology

Brown marmorated stink bug, *Halyomorpha halys* (Stål), an invasive pest species native to Asia was introduced to North America in the 1990's. It has caused significant losses to a wide range of agricultural crops. *H. halys* is a nuisance pest invading homes and structures where it overwinters. I explore host use of *H. halys* on 254 cultivars of woody ornamental plants grown at commercial nurseries in Maryland. Overall, 88 host and 43 non-host cultivars were identified. Angiosperms supported greater abundances of *H. halys* than gymnosperms. Asian cultivars housed fewer *H. halys* than non-Asian cultivars. This trend was strongest in *Acer*, *Ulmus*, and *Pyrus*. Plants native to the invaded realm appear at greater risk to invasive pests than plants in the invaders aboriginal realm. Identifying cultivars most used and least used

by *H. halys* enables growers to sell refractory cultivars making landscapes less supportive to *H. halys* and more sustainable.

PATTERNS OF HOST USE BY BROWN MARMORATED STINK BUG,
HALYOMORPHA HALYS (HEMIPTERA: PENTATOMIDAE) IN WOODY
ORNAMENTAL TREES AND SHRUBS

By

Erik John Bergmann

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Advisory Committee:
Professor Michael J. Raupp, Chair
Associate Professor Paula M. Shrewsbury
Associate Professor Daniel S. Gruner

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Dedication

I dedicate this work to my incredible parents,
John and Leslie, for their continuous love and support.

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I would like to thank all the people that have helped me throughout the duration of my graduate career, first, my advisor Michael Raupp. I started working for Mike as an undergraduate and by the end of that first week I was hooked. He has been an amazing source of knowledge, guidance, and enthusiasm over the past four years. His perspective has been invaluable on all things personal and professional.

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Chapter 1: Host Breadth of the Brown Marmorated Stink Bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), utilizing Woody Ornamental Trees and Shrubs.

Abstract

In this chapter I focus on the identification of hosts and non-hosts of *H. halys*. This study surveyed 254 cultivars of woody ornamental plants grown in commercial nurseries in Maryland. I found 88 host cultivars and 43 non-host cultivars of *H. halys*. Angiosperms hosted higher numbers of *H. halys* than gymnosperms. *H. halys* females oviposited on a narrow range of plants. Adult *H. halys* were also found on a wider range of hosts than less mobile nymphs. The identification of these cultivars and patterns of behavior will aid in the design of landscapes refractory to *H. halys* activity. This research may help reduce the number of nuisance *H. halys* entering residential structures from surrounding landscapes. These results may also provide a marketing advantage to growers that produce and sell plants less used by *H. halys* as hosts.

Introduction

The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), an insect native to Japan, China, Taiwan, and Korea, was first discovered in the United States near Allentown, PA in the middle 1990's (Hoebeke and Carter 2003). At the time of this writing *H. halys* has been reported in 42 states, the District of Columbia, and two Canadian provinces in North America (Northeast IPM Center 2015). Beyond North America *H. halys* has invaded several European

countries including Lichtenstein and Switzerland (Wermelinger et al. 2008), France (Callot and Brua 2013), Italy (Pansa et al. 2013), Germany (Heckmann 2012), and Hungary (Vetek et al. 2014).

Halyomorpha halys is highly polyphagous in its native and invaded ranges. An important review of the Asian literature by Lee et al. (2013) revealed 106 hosts distributed in 45 families ranging from herbaceous annual vegetable crops to forest trees. Lee et al. (2013) noted a preponderance of hosts in the Fabaceae and Rosaceae in Asia. In the invaded North American realm, studies conducted by Bernon (2004) in several counties in eastern Pennsylvania recorded *H. halys* on 73 species of plants ranging from annual crops to landscape trees. Trees and shrubs, many of which were non-native to North America, dominated the list of plants upon which *H. halys* was noted as abundant or common (Bernon 2004). A quantitative survey of 13 ornamental and cultivated hosts used by *H. halys* nymphs and adults demonstrated temporal and developmental stage specific shifts in host use over the course of two growing seasons (Nielsen and Hamilton 2009). This study confirmed that at certain times of the season North American hosts such as American ash supported high numbers of *H. halys*. A recent report by Bakken et al. (2015) revealed the greatest numbers of *H. halys* on tree of heaven, catalpa, yellowwood, paulownia, cherry, walnut, and redbud growing in non-managed woodlands in North Carolina and Virginia. In Europe a synthesis by Haye et al. (2014) reported 51 host plants in 32 plant families. This list included European natives and non-native plants ranging from herbaceous perennials to woody trees and shrubs. Among species with the highest observed densities, no clear pattern emerged with respect to plant provenance (Haye et al. 2014).

Direct damage to plants by *H. halys* depends on several factors including the type of crop, its phenological stage and the location of the crop relative to sources of stink bugs (Nielsen and Hamilton 2009, Leskey et al. 2012, Lee et al. 2013, Rice et al. 2014, Martinson et al. 2013, Martinson et al. 2015, Venugopal et al. 2015). Indirect damage can result by the transmission of plant diseases including Paulownia Witches' Broom (Hiruki 1999). In the United States during the growing season of 2010, populations of *H. halys* burgeoned and multimillion dollar losses were recorded on orchard crops including apples and peaches; vegetables such as sweet corn, peppers, and tomatoes; row crops including field corn and soybeans; vineyards; small fruit; and ornamental plants grown in landscape nurseries (Leskey et al. 2012, Martinson et al. 2013, 2015, Rice et al. 2014). In addition to crop damage, *H. halys* is a severe nuisance pest during fall, winter, and spring when adults aggregate on commercial buildings and homes, enter and overwinter in domiciles, and egress in spring (Bernon 2004, Hamilton 2009, Cooper 2010, Inkley 2012, Haye et al. 2014, Rice et al. 2014). These behaviors generated public concern, media attention, and a general outcry for management solutions (Inkley 2012, Haye et al. 2014, Rice et al. 2014). In response to this demand pest control companies provide services including the treatment of buildings and landscape plants where *H. halys* aggregate in autumn prior to entering structures (Cooper 2010).

Several of the aforementioned reviews of *H. halys* noted significant variation in patterns of host use in woody landscape plants. However, these reviews focused on plants on which *H. halys* was observed feeding or breeding, but with the exception of the survey by Bakken et al. (2015) little or no information was presented on the plants

that were not used as hosts by *H. halys*. The use of resistant plant material is a mainstay of integrated pest management for agronomic crops (Painter 1951, Maxwell and Jennings 1980) as well as ornamental plants in landscapes (Potter 1986, Raupp et al. 1992, Herms 2002). The primary goal of this study was to identify ornamental woody plants grown by the nursery industry for use in landscaping that are not included in the feeding or breeding repertoire of *H. halys*. Incorporating plants not used by *H. halys* into landscapes could reduce breeding sites and places where stink bugs aggregate prior to entering homes, thereby reducing the need for treating plants with insecticides to kill this pest in landscapes (Cooper et al. 2010). Moreover, by identifying ornamental plants refractory to this pest, commercial growers of landscape plants could enjoy a marketing advantage by producing and selling plants that reduce the likelihood of autumnal home invasions.

In this study I examined patterns of host use by *H. halys* in large, diverse, commercial production nurseries in Maryland. Of particular interest was the identification of plants not used by any life stage, particularly ovipositing females. Previous studies of host use by *H. halys* noted significant intraspecific variation among varieties of tree fruits (Fujisawa 2001, Zhang et al. 2007, Funayama 2015). I endeavored to see if similar intraspecific variation existed in woody ornamental plants growing in commercial nurseries. Several Asian studies and reviews by Lee et al. (2013) and Haye et.al. (2014) noted *H. halys* utilizing many species of gymnosperms, however, gymnosperms were conspicuously lacking in host lists from North America (Bernon 2004, Nielsen and Hamilton 2009, Bakken et al 2015). Commercial nurseries in this study provided a rich source of familial, generic,

specific, and varietal variation in which to explore patterns of host use by *H. halys* on angiosperms and gymnosperms grown for installation in residential landscapes.

Materials and Methods

Study Design and Data Collection

During a 3 year period *H. halys* was sampled in two commercial woody plant nurseries located in Frederick and Montgomery Counties, MD. Timed visual surveys of *H. halys* life stages were recorded in each nursery on trees and shrubs on multiple occasions each year. Surveys conducted in 2011 occurred at several production fields at Raemelon Farm in Adamstown in western MD (39.29 latitude; 77.47 longitude) and in 2012 and 2013, surveys were conducted at several production fields at Raemelon Farm and Ruppert Nurseries in Laytonsville in central MD (39.212633; 77.142759). Production fields at Ruppert Nurseries consisted of 20 rows of 25–35 ornamental trees and shrubs. Raemelon fields were larger and consisted of 80–150 rows. Rows at both locations were spaced approximately 3 m apart and depending on the size of the plant, plants within rows were approximately 2 m apart. Plants ranged in height from 1 to 4 m. Six trees of each cultivar were surveyed in each row. These nurseries were planted with a wide variety of trees. Specifically, single cultivars were typically planted within a row, but fields differed in cultivar composition.

Data Collection and Tree Identification

Following the protocols of Venugopal et al. (2015) and Martinson et al. (2015) 1-min visual counts of *H. halys* were conducted on foliage, flowers, fruits/seeds, and bark to a height of up to 3 m. To ensure uniformity and consistency in the field protocols for data collection everyone involved in the collection of data

where trained by me and M.J.R. *H. halys* abundance was recorded separately for four life stages: egg masses, early instar nymphs (instars 1 – 3), late instar nymphs (instars 4 and 5), and adults. Each year, repeated counts were conducted at each tree in early June, late June, mid-July, and early August. Some sampled trees were sold during the study period; tree mortality from heat stress, disease, and physical damage also resulted in variable numbers of readings or ‘tree visits’ for some trees (see Table 1 for number of visits for each cultivar). Tree genus, species, and cultivar, if applicable, were recorded. Identification was completed using nursery records and confirmed using existing literature (Dirr 2009, The Plant List 2013) to ensure consistent usage of cultivar names, common names, and spellings.

Statistical Analysis

Host use by different life stages

Cultivars on which all four life stages (egg masses, early and late nymphs, and adults) of *H. halys* were observed were categorized as hosts. The concept of ‘host’ has been used in several contexts. With respect to *H. halys*, Nielsen and Hamilton (2009) classified plants as hosts if consecutive nymphal stages were observed across multiple years. The presence of all life stages indicate the suitability of the cultivar for adult oviposition and nymphal development, thereby representing reproductive host status for stink bugs (Velasco and Walter 1992, Panizzi 1997). In this study species and varieties where eggs, nymphs, and adults were observed were classified as hosts. On the other hand, species and cultivars on which no life stages were recorded were categorized as non-hosts. Species and cultivars on which one but not

all life stages were observed were classified as partial hosts. The designations of host use for each stadium are summarized in Table 1.

To test whether host use was similar across all life stages of *H. halys*, I calculated the proportion of cultivars used by each life stage. I used a Fisher's exact test for pairwise (each life stage) statistical comparisons of these proportions. The hosts were further ranked based on the density of *H. halys* observed per cultivar, calculated as per the equation below:

$$H. halys \text{ density} = \frac{\text{Summed count of nymph and adult } H. halys \text{ on cultivar}}{(\text{Number of individual trees of cultivar} \times \text{Total number of visits to each tree})}$$

Use of angiosperms and gymnosperms

The use of angiosperms and gymnosperms by *H. halys* was analyzed through generalized linear models (GLM) assuming a Quasi-Poisson error distribution and log link function (VerHoef and Boveng 2007). GLMs were performed for each life stage with the abundance of *H. halys* as the response variable and taxonomic status as an angiosperm compared to gymnosperm as the predictor, accounting for differences in tree visits across the cultivars (through 'offset' statement). Significant differences in the model estimated means were identified through Tukey's HSD comparisons ($\alpha = 0.05$).

All statistical analyses were performed in R program (R Development Core Team 2014) and associated statistical packages. Tukey's HSD were performed with the package "multcomp" (Hothorn et al. 2008). Package "Vennrable" (Swinton 2009) was used for plotting the Venn diagram and GLMs estimated coefficients were extracted and plotted using "ggplot2" (Wickham 2009).

Results

Host use by different life stages

Over all three years and the 254 unique cultivars of ornamental trees and shrubs sampled, *H. halys* was recorded on 211 (83%) cultivars. Egg masses were present on 99 (39%) cultivars, nymphs (including both early and late instars) on 181 (71%) cultivars and adults on 198 (78%) cultivars (Fig. 1). The proportions of cultivars used by each *H. halys* life stage were significantly different from each other based on the pairwise comparisons (egg mass vs. early nymphs, egg mass vs. late nymphs, egg mass vs. adults, early nymphs vs. late nymphs, early nymphs vs. adults, late nymphs vs. adults; Fisher's Exact test; $P < 0.001$). There were no cultivars on which only the egg mass and no other stages was recorded. Similarly, there were very few cultivars with egg mass and nymphs without adults, and egg mass and adults without records of nymphs (Fig. 1). On 88 cultivars, at least one individual of each *H. halys* life stage was recorded and these were classified as hosts, whereas the 43 cultivars with no records of stink bugs were classified as non-hosts. The remaining 123 cultivars were classified as partial hosts by virtue of the presence on at least one but not all life stages (see Table 1). Table 2 presents the 25 cultivars most frequently used by *H. halys* and the density of *H. halys* found on each cultivar. Notably, maples (Family Sapindaceae) and legumes (Family Leguminosae) constituted half of these top 25 cultivars. Conversely, stink bugs were not recorded on 43 (17%) cultivars (non-hosts). Among these non-hosts, cultivars of the pine family (Family Pinaceae) were the most frequently reported (20 cultivars; Table 3). Table 1 provides a

summary of the numbers of each life stage found on each host over the course of the study.

Use of Angiosperms and Gymnosperms

Results of the GLM and Tukey's HSD revealed that across all the life stages, significantly higher abundances of *H. halys* were observed on angiosperms than gymnosperms (Tukey's HSD: $P < 0.05$) (Fig. 2). *H. halys* abundance ranged from 5 to 15 times higher for adults, nymphs, and egg masses on angiosperms compared to gymnosperms.

Discussion

My results agree with previous work in North America (Bernon 2004, Nielsen and Hamilton 2009, Bakken et al. 2015), Asia (Lee et al. 2013), and Europe (Haye et al. 2014) who observed one or more life stages of *H. halys* on a broad range of woody plants in managed and non-managed settings. Genera common to these previous studies and this study include *Acer*, *Aesculus*, *Amelanchier*, *Betula*, *Carpinus*, *Carya*, *Cedrus*, *Celtis*, *Cercis*, *Cladrastis*, *Crataegus*, *Cryptomeria*, *Cupressus*, *Ficus*, *Forsythia*, *Ginkgo*, *Hamamelis*, *Hibiscus*, *Ilex*, *Koelreutaria*, *Liquidambar*, *Magnolia*, *Malus*, *Platanus*, *Prunus*, *Rhus*, *Pyrus*, *Sambucus*, *Stewartia*, *Syringa*, *Tilia*, *Ulmus*, *Viburnum*, and *Zelkova*. Genera of woody plants utilized by *H. halys* listed in previous works but not sampled in my nurseries include *Ailanthus*, *Aralia*, *Aronia*, *Asimina*, *Buddleia*, *Camelli*, *Campsis*, *Caragana*, *Castanea*, *Catalpa*, *Celastrus*, *Cephalanthus*, *Chaenomeles*, *Cinnamomum*, *Citrus*, *Clerodendrum*, *Corylus*, *Cotoneaster*, *Decaisnea*, *Diospyros*, *Elaeagnus*, *Euonymus*, *Fraxinus*, *Juglans*, *Lagerstroemia*, *Laurus*, *Ligustrum*, *Liriodendron*, *Lonicera*, *Mimosa*, *Morus*, *Nerium*,

Olea, *Paulownia*, *Populus*, *Platycladus*, *Punica*, *Pyracantha*, *Rhus*, *Robinia*, *Rosa*, *Salix*, *Sassafras*, *Sequoia*, *Spiraea*, *Sorbus*, *Toona*, *Trachycarpus*, *Vitex*, *Weigela*, *Wisteri*, and *Ziziphus* (Bernon 2004, Nielsen and Hamilton 2009, Lee et al. 2013, Haye et al. 2014, Bakken et al. 2015).

Favored hosts found in this study match those of previous ones for several genera (Table 2). *Prunus* is a genus that appears on my list of the 25 most utilized hosts and other lists of common hosts for *H. halys* (Bernon 2004, Bakken et al. 2015). Other genera found on my list of the 25 most commonly used that appear on other lists include *Malus* (Bernon 2004), *Syringa* (Bernon 2004), *Acer* (Bernon 2004), *Cladrastis* (Bakken et al. 2015) and *Cercis* (Bakken et al. 2015). Lee et al. (2013) noted the affinity of *H. halys* for hosts in the Fabaceae and Rosaceae. In addition to these families, Oleaceae, Sapindaceae, Rutaceae, Ulmaceae, Moraceae, Altingiaceae, and Malvaceae supported the greatest abundances of *H. halys* over three years of this study (Table 2). Funayama (2002) noted the importance of multiple hosts in the normal development of *H. halys*. Recent work by Martinson et al. (2015) demonstrated the strong positive relationship between the presence of fruit and the abundance of *H. halys* adults on individual trees. Several studies including those of Leskey et al. (2012), Lee et al. (2013), and Venugopal et al. (2015) detailed the ability of *H. halys* to track high quality resources in time and space. This explains at least in part the pattern of broad host use in *H. haly* as different species and cultivars presented resources of differing quality in the nurseries throughout the growing season.

Pursuant of my primary objective to identify species and cultivars not used for oviposition or feeding, I identified 43 unique cultivars in 17 genera Table 3. These genera with the corresponding number of non-host cultivars (parenthetically) were: *Abies* (1), *Acer* (7), *Aesculus* (1), *Cedrus* (2), *Cercidiphyllum* (1), *Chamaecyparis* (4), *Cornus* (1), *Ginkgo* (1), *Hamamelis* (2), *Juniperus* (1), *Physocarpus* (1), *Picea* (9), *Pinus* (7), *Prunus* (2), *Sequoiadendron* (1), *Thuja* (1), and *Tsuga* (1). These patterns of intraspecific variation in host use mirror those of other studies that demonstrate variation in host use among varieties of apples. Fujisawa (2001) and Funayama (2002) attributed intraspecific variation in patterns of host use to differences in fruiting times among cultivars of apples. This intraspecific variation is a potentially useful source of identifying varieties resistant to *H. halys*. In this study early fruiting cultivars of shrubs like *Hamamelis x intermedia* or non-fruiting trees such as male *Ginkgo biloba* ‘Saratoga’ were devoid of all life stages of *H. halys* and classified as non-hosts. Flowering and fruiting of *Hamamelis* occurs in winter and early spring, well in advance of the arrival of *H. halys* into the nursery (Venugopal et al. 2015, Martinson et al. 2015). In interpreting my designation of varieties as non-hosts, I urge caution for several cultivars listed as such due to the relatively small number of observations associated with some varieties. For example, the number of observations of *Acer davidii* was four over the entire course of the study and due to the small number of tree visits, the placement of this species as a non-host is not well-supported (Table 1). By contrast *Acer davidii*’s congener *Acer palmatum* var. *dissectum* ‘Inaba Shidare’ was observed 144 times over the three years of the study and its designation as a non-host is well-supported (Table 1).

This report confirms the use of several families, genera, species, and cultivars of gymnosperms as hosts for *H. halys* in North America (Table 1). The use of gymnosperms is well established in the Asian literature (Oda et al. 1980, Yanagi and Hagihara 1980, Kawada and Kitamura 1983, Qin 1990, Fujisawa 2001, Funayama 2002, 2005, Yu and Zhang 2007, Lee et al. 2013) and some gymnosperms such as Japanese cedar serve as important hosts for overwintered adults early in the season (Funayama 2005, Lee et al. 2013). Although, gymnosperms are used as hosts by *H. halys*, it is noteworthy that gymnosperms housed far fewer *H. halys* than angiosperms (Fig. 2). Moreover, the list of non-hosts was dominated by gymnosperms particularly those in the Pinaceae and Cupressaceae where families contained several genera and species of non-hosts. Another important finding of the study is that host use varies dramatically within genera and species. For example, *H. halys* was never observed on several varieties of *Acer palmatum* while most cultivars of its congener *Acer rubrum* were heavily utilized. Several species of *Ginkgo biloba* supported notable numbers of *H. halys* nymphs and adults whereas *Ginkgo biloba* ‘Saratoga’ supported none.

Stage specific differences in patterns of host use in this study reflect those found in previous studies of *H. halys* on woody plants. Nielsen and Hamilton (2009) noted stage specific shifts in host use as different instars of *H. halys* tracked resources on different woody hosts. In non-managed settings in several locations in North Carolina and Virginia, Bakken et al. (2015) reported the broadest range of hosts used by adult *H. halys*, the fewest hosts used as oviposition sites, and nymphs utilizing many more hosts than ovipositing females, but slightly fewer hosts than adults. I found ovipositing females to use the fewest numbers of hosts whereas highly mobile

adults were found on the greatest number. Early and late instar nymphs were found on intermediate numbers of hosts with older instars utilizing more hosts than younger ones.

The practical implications of this study are that several species and cultivars presently in production do not appear to be utilized by any life stage of *H. halys* and by my definition they are not hosts. By planting these varieties in landscapes landowners may enjoy lower levels of *H. halys* in their landscapes with the additional benefit of spawning fewer *H. halys* that will become nuisance pests as they enter homes and businesses in autumn. In a recent review (Clapp et al. 2014) recommended the use of gymnosperms in landscape plantings as a means of diversifying the urban forest with trees that provide valuable ecosystem services including water infiltration, carbon sequestration, and as a buffer against invasive species. My findings provide evidence that gymnosperms provide a rich source of plant material refractory to *H. halys* for use in landscapes. Growers who produce these resistant varieties may enjoy a marketing advantage in states and countries within the invaded range of *H. halys*.

Table 1. List of ornamental tree and shrub cultivars sampled and the abundance of different life stages of *Halyomorpha halys*.

See methods for details on the host, non-host, and partial host status classification. Column 1, No. = cultivar number.

No.	Species	Cultivar	Family	Classification	Tree Visits	Egg Mass	Early Nymphs	Late Nymphs	Adults	Host Status
1	<i>Abies koreana</i> E.H.Wilson		Pinaceae	Gymnosperm	636	0	3	0	8	partial
2	<i>Abies nordmanniana</i> (Steven) Spach	Ambrolauria	Pinaceae	Gymnosperm	18	0	0	0	2	partial
3	<i>Abies nordmanniana</i> (Steven) Spach		Pinaceae	Gymnosperm	72	0	0	0	0	non-host
4	<i>Acer campestre</i> L.	Evelyn	Sapindaceae	Angiosperm	288	5	235	23	119	host
5	<i>Acer davidii</i> Franch.		Sapindaceae	Angiosperm	4	0	0	0	0	non-host
6	<i>Acer griseum</i> (Franch.) Pax		Sapindaceae	Angiosperm	396	1	88	13	29	host
7	<i>Acer palmatum</i> Thunb.	Bloodgood	Sapindaceae	Angiosperm	243	2	2	0	35	partial
8	<i>Acer palmatum</i> Thunb.	Emperor I	Sapindaceae	Angiosperm	72	0	0	0	0	non-host
9	<i>Acer palmatum</i> Thunb.	Moonfire	Sapindaceae	Angiosperm	48	0	0	0	0	non-host
10	<i>Acer palmatum</i> Thunb.	Red Emperor	Sapindaceae	Angiosperm	263	2	3	0	15	partial

11	<i>Acer palmatum</i> Thunb.	Sango Kaku	Sapindaceae	Angiosperm	96	0	0	0	0	non-host
12	<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Crimson Queen	Sapindaceae	Angiosperm	24	0	0	0	0	non-host
13	<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Inaba Shidare	Sapindaceae	Angiosperm	144	0	0	0	0	non-host
14	<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Seiryu	Sapindaceae	Angiosperm	18	0	0	0	0	non-host
15	<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Viridis	Sapindaceae	Angiosperm	90	0	0	0	1	partial
16	<i>Acer pensylvanicum</i> L.		Sapindaceae	Angiosperm	32	1	58	6	17	host
17	<i>Acer rubrum</i> L.	Armstrong	Sapindaceae	Angiosperm	282	5	366	154	6	host
18	<i>Acer rubrum</i> L.	Bowhall	Sapindaceae	Angiosperm	216	2	369	16	18	host
19	<i>Acer rubrum</i> L.	Brandywine	Sapindaceae	Angiosperm	528	19	829	92	99	host
20	<i>Acer rubrum</i> L.	Franksred	Sapindaceae	Angiosperm	1530	40	1829	299	145	host
21	<i>Acer rubrum</i> L.	October Glory	Sapindaceae	Angiosperm	960	22	1352	305	51	host
22	<i>Acer rubrum</i> L.	Sun Valley	Sapindaceae	Angiosperm	72	0	62	12	0	partial
23	<i>Acer rufinerve</i> Siebold & Zucc.		Sapindaceae	Angiosperm	84	0	69	0	0	partial
24	<i>Acer saccharum</i> Marshall	Commemorati on	Sapindaceae	Angiosperm	192	3	169	22	9	host
25	<i>Acer saccharum</i> Marshall	Green Mountain	Sapindaceae	Angiosperm	1625	32	1401	240	163	host
26	<i>Acer saccharum</i> Marshall	Legacy	Sapindaceae	Angiosperm	524	17	503	18	18	host

27	<i>Acer truncatum</i> Bunge		Sapindaceae	Angiosperm	72	0	1	0	4	partial
28	<i>Acer x freemanii</i>	Jeffersred	Sapindaceae	Angiosperm	117	4	347	20	19	host
29	<i>Acer x tegmentosum</i>	White Tigress	Sapindaceae	Angiosperm	108	0	63	3	1	partial
30	<i>Aesculus hippocastanum</i> L.	baumannii	Sapindaceae	Angiosperm	6	0	0	0	0	non-host
31	<i>Aesculus x carnea</i>	Briotii	Sapindaceae	Angiosperm	276	0	6	1	15	partial
32	<i>Aesculus x carnea</i>	Fort McNair	Sapindaceae	Angiosperm	270	3	69	1	47	host
33	<i>Amelanchier x grandiflora</i>	Autumn Brilliance	Rosaceae	Angiosperm	860	14	737	82	219	host
34	<i>Amelanchier x grandiflora</i>	Princess Diana	Rosaceae	Angiosperm	300	2	64	20	42	host
35	<i>Betula nigra</i> L.	BNMTF	Betulaceae	Angiosperm	333	2	141	8	25	host
36	<i>Betula nigra</i> L.	Cully	Betulaceae	Angiosperm	84	2	11	0	3	partial
37	<i>Betula nigra</i> L.	Heritage	Betulaceae	Angiosperm	84	2	35	1	0	partial
38	<i>Betula papyrifera</i> Marshall	Renci	Betulaceae	Angiosperm	138	1	68	2	29	host
39	<i>Calocedrus decurrens</i> (Torr.) Florin		Cupressaceae	Angiosperm	120	0	3	0	8	partial
40	<i>Carpinus betulus</i> L.	Fastigiata	Betulaceae	Angiosperm	770	10	451	17	30	host
41	<i>Carpinus betulus</i> L.	Frans Fontaine	Betulaceae	Angiosperm	228	0	27	1	31	partial

42	<i>Carya illinoensis</i> (Wangenh.) K.Koch	Choctaw	Juglandaceae	Angiosperm	48	0	19	4	66	partial
43	<i>Cedrus atlantica</i> (Endl.) Manetti ex Carrière	Glaucia	Pinaceae	Gymnosperm	234	0	0	0	2	partial
44	<i>Cedrus atlantica</i> (Endl.) Manetti ex Carrière	Kroh's Twisted	Pinaceae	Gymnosperm	75	0	0	0	0	non-host
45	<i>Cedrus deodara</i> (Roxb. ex D.Don) G.Don	Karl Fuchs	Pinaceae	Gymnosperm	72	0	0	0	0	non-host
46	<i>Cedrus deodara</i> (Roxb. ex D.Don) G.Don	Shalimar	Pinaceae	Gymnosperm	96	0	4	0	6	partial
47	<i>Celtis koraiensis</i> Nakai		Cannabaceae	Angiosperm	12	0	0	1	6	partial
48	<i>Cercidiphyllum japonicum</i> Siebold & Zucc. ex J.J.Hoffm. & J.H.Schult.bis	Red Fox	Cercidiphyllaceae	Angiosperm	10	0	0	0	0	non-host
49	<i>Cercidiphyllum japonicum</i> Siebold & Zucc. ex J.J.Hoffm. & J.H.Schult.bis		Cercidiphyllaceae	Angiosperm	317	1	321	9	98	host

50	<i>Cercis canadensis</i> L.	Alba	Leguminosae	Angiosperm	96	0	123	25	125	partial
51	<i>Cercis canadensis</i> L.	Appalachian Red	Leguminosae	Angiosperm	168	5	85	2	14	host
52	<i>Cercis canadensis</i> L.	Covey	Leguminosae	Angiosperm	162	3	88	10	53	host
53	<i>Cercis canadensis</i> L.	Forest Pansy	Leguminosae	Angiosperm	222	3	160	15	82	host
54	<i>Cercis canadensis</i> L.	Pink Heartbreaker	Leguminosae	Angiosperm	96	0	116	3	42	partial
55	<i>Cercis canadensis</i> L.		Leguminosae	Angiosperm	360	16	707	55	57	host
56	<i>Chamaecyparis nootkatensis</i> D.Don	Pendula	Cupressaceae	Gymnosperm	438	0	0	0	26	partial
57	<i>Chamaecyparis nootkatensis</i> D.Don	Pendula Glauca	Cupressaceae	Gymnosperm	66	0	1	0	0	partial
58	<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Aurea Nana	Cupressaceae	Gymnosperm	45	0	0	0	0	non-host
59	<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Compacta	Cupressaceae	Gymnosperm	66	0	0	0	0	non-host
60	<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Crippsii	Cupressaceae	Gymnosperm	258	0	0	0	1	partial
61	<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Gimborn's Beauty	Cupressaceae	Gymnosperm	27	0	0	0	0	non-host

62	<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Kosteri	Cupressaceae	Gymnosperm	27	0	0	0	0	non-host
63	<i>Chionanthus retusus</i> Lindl. & Paxton		Oleaceae	Angiosperm	204	0	1	4	26	partial
64	<i>Cladrastis kentukea</i> (Dum.Cours.) Rudd	Perkins Pink	Leguminosae	Angiosperm	219	8	289	15	23	host
65	<i>Cladrastis kentukea</i> (Dum.Cours.) Rudd		Leguminosae	Angiosperm	450	17	570	105	145	host
66	<i>Cornus controversa</i> Hemsl.		Cornaceae	Angiosperm	162	0	2	17	48	partial
67	<i>Cornus florida</i> L.	Appalachian Spring	Cornaceae	Angiosperm	198	0	38	0	10	partial
68	<i>Cornus florida</i> L.	Cherokee Princess	Cornaceae	Angiosperm	452	0	78	1	38	partial
69	<i>Cornus florida</i> L.	Cloud 9	Cornaceae	Angiosperm	186	0	22	6	11	partial
70	<i>Cornus florida</i> L.	COMCO #1	Cornaceae	Angiosperm	405	0	59	1	32	partial
71	<i>Cornus florida</i> L.	Jean's Appalachian Snow	Cornaceae	Angiosperm	132	0	1	0	33	partial
72	<i>Cornus florida</i> L.	Kay's Appalachian Mist	Cornaceae	Angiosperm	132	0	3	0	12	partial
73	<i>Cornus florida</i> L.		Cornaceae	Angiosperm	12	0	3	0	9	partial

74	<i>Cornus florida</i> x <i>kousa</i> L.	Aurora	Cornaceae	Angiosperm	75	0	0	1	0	partial
75	<i>Cornus florida</i> x <i>kousa</i> L.	Celestial	Cornaceae	Angiosperm	21	0	21	0	24	partial
76	<i>Cornus florida</i> x <i>kousa</i> L.	Constellation	Cornaceae	Angiosperm	73	0	16	0	13	partial
77	<i>Cornus florida</i> x <i>kousa</i> L.	Ruth Ellen	Cornaceae	Angiosperm	36	0	22	0	4	partial
78	<i>Cornus florida</i> x <i>kousa</i> L.	Stellar Pink	Cornaceae	Angiosperm	212	1	30	1	21	host
79	<i>Cornus kousa</i> F.Buerger ex Hance	Madison	Cornaceae	Angiosperm	80	0	2	0	7	partial
80	<i>Cornus kousa</i> F.Buerger ex Hance	National	Cornaceae	Angiosperm	108	0	26	3	7	partial
81	<i>Cornus kousa</i> F.Buerger ex Hance	Radiant Rose	Cornaceae	Angiosperm	16	0	0	0	0	non-host
82	<i>Cornus kousa</i> F.Buerger ex Hance	Santomi	Cornaceae	Angiosperm	570	0	83	19	34	partial
83	<i>Cornus kousa</i> var <i>chinensis</i>	Milky Way	Cornaceae	Angiosperm	315	0	6	2	31	partial
84	<i>Cornus</i> <i>macrophylla</i> Wall.		Cornaceae	Angiosperm	168	4	95	14	44	host
85	<i>Cornus</i> <i>officinalis</i> Siebold & Zucc.		Cornaceae	Angiosperm	252	0	4	3	31	partial

86	<i>Cornus walteri</i> Wangerin		Cornaceae	Angiosperm	84	0	30	0	15	partial
87	<i>Crataegus</i> <i>crusgalli</i> L.	Cruzam	Rosaceae	Angiosperm	12	0	0	0	1	partial
88	<i>Crataegus</i> <i>laevigata</i> (Poir.) DC.	Superba	Rosaceae	Angiosperm	135	1	24	2	7	host
89	<i>Crataegus</i> <i>phaenopyrum</i> (L.f.) Medik.		Rosaceae	Angiosperm	123	0	24	2	4	partial
90	<i>Crataegus viridis</i> L.	Winter King	Rosaceae	Angiosperm	948	6	325	26	50	host
91	<i>Cryptomeria</i> <i>japonica</i> (Thunb. ex L.f.) D.Don	Black Dragon	Cupressaceae	Gymnosperm	153	0	0	0	4	partial
92	<i>Cryptomeria</i> <i>japonica</i> (Thunb. ex L.f.) D.Don	Gyokuryu	Cupressaceae	Gymnosperm	180	0	0	0	1	partial
93	<i>Cryptomeria</i> <i>japonica</i> (Thunb. ex L.f.) D.Don	Yoshino	Cupressaceae	Gymnosperm	309	0	37	1	122	partial
94	<i>Cryptomeria</i> <i>japonica</i> (Thunb. ex L.f.) D.Don		Cupressaceae	Gymnosperm	72	0	21	1	3	partial
95	<i>Cupressocyparis</i> <i>leylandii</i> A.B.Jacks. & Dallim.		Cupressaceae	Gymnosperm	96	0	36	2	10	partial

96	<i>Evodia daniellii</i> (Benn.) T.G.Hartley		Rutaceae	Angiosperm	12	9	15	9	19	host
97	<i>Evodia hupehensis</i> (Benn.) T.G.Hartley		Rutaceae	Angiosperm	180	4	176	75	69	host
98	<i>Ficus carica</i> L.	Chicago Hardy	Moraceae	Angiosperm	45	2	3	6	78	host
99	<i>Ginkgo biloba</i> L.	Autumn Gold	Ginkgoaceae	Gymnosperm	384	4	38	0	25	partial
100	<i>Ginkgo biloba</i> L.	Magyar	Ginkgoaceae	Gymnosperm	240	0	0	0	19	partial
101	<i>Ginkgo biloba</i> L.	Princeton Sentry	Ginkgoaceae	Gymnosperm	288	7	93	0	9	host
102	<i>Ginkgo biloba</i> L.	Saratoga	Ginkgoaceae	Gymnosperm	72	0	0	0	0	non-host
103	<i>Gleditsia triacanthos</i> L.	Shademaster	Leguminosae	Angiosperm	1248	13	589	155	469	host
104	<i>Gleditsia triacanthos</i> L.	Skyline	Leguminosae	Angiosperm	282	2	119	64	22	host
105	<i>Halesia tetraptera</i> L.	Arnold Pink	Styracaceae	Angiosperm	12	0	0	2	5	partial
106	<i>Halesia tetraptera</i> L.		Styracaceae	Angiosperm	390	4	173	12	55	host
107	<i>Hamamelis x intermedia</i>	Arnold Promise	Hamamelidaceae	Angiosperm	249	0	1	0	14	partial
108	<i>Hamamelis x intermedia</i>	Diane	Hamamelidaceae	Angiosperm	201	0	24	0	9	partial
109	<i>Hamamelis x intermedia</i>	Jelena	Hamamelidaceae	Angiosperm	42	0	0	0	0	non-host
110	<i>Hamamelis x intermedia</i>	Pallida	Hamamelidaceae	Angiosperm	12	0	0	0	0	non-host

111	<i>Heptacodium miconioides</i> Rehder		Caprifoliaceae	Angiosperm	185	0	8	1	14	partial
112	<i>Hibiscus syriacus</i> L.	Blue Bird	Malvaceae	Angiosperm	132	0	24	8	116	partial
113	<i>Hibiscus syriacus</i> L.	Diana	Malvaceae	Angiosperm	60	0	0	1	12	partial
114	<i>Hibiscus syriacus</i> L.	Red Heart	Malvaceae	Angiosperm	126	0	51	40	105	partial
115	<i>Hibiscus syriacus</i> L.	Satin Blue	Malvaceae	Angiosperm	156	0	40	24	287	partial
116	<i>Hibiscus syriacus</i> L.	Satin Rose	Malvaceae	Angiosperm	8	0	4	4	5	partial
117	<i>Hibiscus syriacus</i> L.	White Chiffon	Malvaceae	Angiosperm	4	0	1	0	0	partial
118	<i>Ilex opaca</i> Aiton	Jersey Princess	Aquifoliaceae	Angiosperm	84	0	10	1	1	partial
119	<i>Ilex x aquipernyi</i>	Meschick	Aquifoliaceae	Angiosperm	360	0	27	5	3	partial
120	<i>Juniperus chinensis</i> L.	Torulosa	Cupressaceae	Gymnosperm	72	0	0	0	0	non-host
121	<i>Koelreuteria paniculata</i> Laxm.		Sapindaceae	Angiosperm	670	16	483	85	506	host
122	<i>Larix kaempferi</i> (Lamb.) Carrière		Pinaceae	Gymnosperm	66	0	0	0	1	partial
123	<i>Larix leptolepis</i> (Lamb.) Carrière		Pinaceae	Gymnosperm	20	0	3	0	1	partial
124	<i>Liquidambar styraciflua</i> L.	Cherokee	Altingiaceae	Angiosperm	132	1	9	1	1	host
125	<i>Liquidambar styraciflua</i> L.	Hapdell	Altingiaceae	Angiosperm	29	0	0	0	17	partial

126	<i>Liquidambar styraciflua</i> L.	Moraine	Altingiaceae	Angiosperm	198	3	52	5	50	host
127	<i>Liquidambar styraciflua</i> L.	Rotundiloba	Altingiaceae	Angiosperm	96	3	29	0	3	partial
128	<i>Liquidambar styraciflua</i> L.	Ward	Altingiaceae	Angiosperm	48	1	1	14	1	host
129	<i>Liquidambar styraciflua</i> L.		Altingiaceae	Angiosperm	96	5	108	3	58	host
130	<i>Magnolia liliiflora</i> x <i>stellata</i>	Ann	Magnoliaceae	Angiosperm	84	0	3	0	6	partial
131	<i>Magnolia liliiflora</i> x <i>stellata</i>	Merrill	Magnoliaceae	Angiosperm	78	0	4	2	39	partial
132	<i>Magnolia</i> x <i>loebneri</i>	Leonard Messel	Magnoliaceae	Angiosperm	84	0	40	0	2	partial
133	<i>Malus</i>	Adams	Rosaceae	Angiosperm	144	2	95	40	3	host
134	<i>Malus</i>	Donald Wyman	Rosaceae	Angiosperm	384	2	248	53	361	host
135	<i>Malus</i>	Mary Potter	Rosaceae	Angiosperm	33	1	31	3	38	host
136	<i>Malus</i>	Molten Lava	Rosaceae	Angiosperm	300	3	137	15	245	host
137	<i>Malus</i>	Pink Princess	Rosaceae	Angiosperm	264	1	11	10	56	host
138	<i>Malus</i>	Prairifire	Rosaceae	Angiosperm	756	24	293	94	259	host
139	<i>Malus</i>	Spring Snow	Rosaceae	Angiosperm	72	0	34	0	0	partial
140	<i>Malus baccata</i> (L.) Borkh.	Jackii	Rosaceae	Angiosperm	15	0	5	1	1	partial
141	<i>Malus domestica</i> Borkh.	Crimson Crisp	Rosaceae	Angiosperm	72	0	2	3	98	partial
142	<i>Malus domestica</i> Borkh.	Freedom	Rosaceae	Angiosperm	240	0	46	4	194	partial

143	<i>Malus domestica</i> Borkh.	Liberty	Rosaceae	Angiosperm	354	1	17	12	192	host
144	<i>Malus halliana</i> Koehne	Adirondack	Rosaceae	Angiosperm	300	3	30	15	134	host
145	<i>Malus sargentii</i> Rehder	Select A	Rosaceae	Angiosperm	456	7	132	26	171	host
146	<i>Malus x zumi</i>	Calocarpa	Rosaceae	Angiosperm	489	5	330	63	166	host
147	<i>Metasequoia</i> <i>glyptostroboides</i> Hu & W.C.Cheng		Cupressaceae	Gymnosperm	177	0	43	1	30	partial
148	<i>Nyssa sylvatica</i> Marshall	Tupelo Tower	Cornaceae	Angiosperm	48	0	45	6	1	partial
149	<i>Nyssa sylvatica</i> Marshall	Wildfire	Cornaceae	Angiosperm	108	0	8	1	34	partial
150	<i>Nyssa sylvatica</i> Marshall		Cornaceae	Angiosperm	168	1	61	7	30	host
151	<i>Ostrya</i> <i>virginiana</i> (Mill.) K.Koch		Betulaceae	Angiosperm	72	0	11	1	2	partial
152	<i>Oxydendrum</i> <i>arboreum</i> (L.) DC.		Ericaceae	Angiosperm	180	2	61	4	22	host
153	<i>Parrotia persica</i> C.A.Mey.	Ruby Vase	Hamamelidaceae	Angiosperm	72	0	2	1	0	partial
154	<i>Parrotia persica</i> C.A.Mey.	Vanessa	Hamamelidaceae	Angiosperm	12	0	0	0	14	partial
155	<i>Parrotia persica</i> C.A.Mey.		Hamamelidaceae	Angiosperm	228	1	26	2	26	host

156	<i>Physocarpus opulifolius</i> (L.) Maxim.	Center Glow	Rosaceae	Angiosperm	12	0	0	0	0	non-host
157	<i>Picea abies</i> (L.) H.Karst.		Pinaceae	Gymnosperm	408	0	29	1	2	partial
158	<i>Picea breweriana</i> S.Watson		Pinaceae	Gymnosperm	15	0	0	0	0	non-host
159	<i>Picea koraiensis</i> Nakai		Pinaceae	Gymnosperm	15	0	0	0	0	non-host
160	<i>Picea meyeri</i> Rehder & E.H.Wilson		Pinaceae	Gymnosperm	66	0	0	0	0	non-host
161	<i>Picea omorika</i> (Pancic) Purk.	Pendula	Pinaceae	Gymnosperm	168	0	0	0	0	non-host
162	<i>Picea omorika</i> (Pancic) Purk.		Pinaceae	Gymnosperm	436	0	0	0	14	partial
163	<i>Picea orientalis</i> (L.) Peterm.	Atrovirens	Pinaceae	Gymnosperm	84	0	0	0	1	partial
164	<i>Picea orientalis</i> (L.) Peterm.	Aurea Compacta	Pinaceae	Gymnosperm	126	0	0	0	7	partial
165	<i>Picea orientalis</i> (L.) Peterm.	Gracillis	Pinaceae	Gymnosperm	60	0	0	0	1	partial
166	<i>Picea pungens</i> Engelm.	Blue Diamond	Pinaceae	Gymnosperm	102	0	1	0	0	partial
167	<i>Picea pungens</i> Engelm.	Fastigiata	Pinaceae	Gymnosperm	54	0	0	0	0	non-host

168	<i>Picea pungens</i> Engelm.	Fat Albert	Pinaceae	Gymnosperm	218	0	1	0	1	partial
169	<i>Picea pungens</i> Engelm.	Glauca	Pinaceae	Gymnosperm	16	0	0	0	0	non-host
170	<i>Picea pungens</i> Engelm.	Glauca Fastigata	Pinaceae	Gymnosperm	8	0	0	0	3	partial
171	<i>Picea pungens</i> Engelm.	Glauca Iseli Fastigata	Pinaceae	Gymnosperm	66	0	0	0	0	non-host
172	<i>Picea pungens</i> Engelm.	Glauca Majestic Blue	Pinaceae	Gymnosperm	78	0	0	0	0	non-host
173	<i>Picea pungens</i> Engelm.	Glauca Van Sikes	Pinaceae	Gymnosperm	286	0	0	0	1	partial
174	<i>Picea pungens</i> Engelm.	Hoopsii	Pinaceae	Gymnosperm	178	0	0	0	0	non-host
175	<i>Pinus bungeana</i> Zucc. ex Endl.		Pinaceae	Gymnosperm	84	0	0	0	1	partial
176	<i>Pinus cembra</i> L.	Chalet	Pinaceae	Gymnosperm	66	0	0	0	0	non-host
177	<i>Pinus cembra</i> L.	Silver Sheen	Pinaceae	Gymnosperm	54	0	37	1	38	partial
178	<i>Pinus densiflora</i> Siebold & Zucc.	Umbraculifera	Pinaceae	Gymnosperm	27	0	0	0	0	non-host
179	<i>Pinus flexilis</i> E.James	Vanderwolf's Pyramid	Pinaceae	Gymnosperm	234	0	0	0	22	partial
180	<i>Pinus koraiensis</i> Siebold & Zucc.	Morris Blue	Pinaceae	Gymnosperm	162	0	1	0	0	partial
181	<i>Pinus koraiensis</i> Siebold & Zucc.		Pinaceae	Gymnosperm	156	0	0	0	0	non-host
182	<i>Pinus nigra</i> J.F.Arnold	Arnold Sentinel	Pinaceae	Gymnosperm	27	0	0	0	0	non-host

183	<i>Pinus parvifolia</i> Siebold & Zucc.		Pinaceae	Gymnosperm	36	0	0	0	0	non-host
184	<i>Pinus strobus</i> L.	Pendula	Pinaceae	Gymnosperm	72	0	0	0	0	non-host
185	<i>Pinus thunbergii</i> Parl.	Thunderhead	Pinaceae	Gymnosperm	36	0	0	0	0	non-host
186	<i>Pinus wallichiana</i> A.B.Jacks.		Pinaceae	Gymnosperm	24	0	0	0	2	partial
187	<i>Platanus x acerifolia</i>	Bloodgood	Platanaceae	Angiosperm	1422	23	1296	67	298	host
188	<i>Platanus x acerifolia</i>	Yarwood	Platanaceae	Angiosperm	228	2	165	8	34	host
189	<i>Prunus avium</i> (L.) L.	BaDa Bing	Rosaceae	Angiosperm	90	0	10	1	35	partial
190	<i>Prunus avium</i> (L.) L.	Stella	Rosaceae	Angiosperm	42	0	20	0	24	partial
191	<i>Prunus cerasifera</i> Ehrh.	Crimson Pointe	Rosaceae	Angiosperm	54	0	0	2	32	partial
192	<i>Prunus cerasifera</i> Ehrh.	Cripoizam	Rosaceae	Angiosperm	288	2	25	11	80	host
193	<i>Prunus cerasifera</i> Ehrh.	Thundercloud	Rosaceae	Angiosperm	352	2	2	11	30	host
194	<i>Prunus cerasus</i> L.	Montmorency	Rosaceae	Angiosperm	48	0	23	5	12	partial
195	<i>Prunus cerasus</i> L.		Rosaceae	Angiosperm	72	0	1	1	7	partial
196	<i>Prunus mume</i> (Siebold) Siebold & Zucc.	Bonita	Rosaceae	Angiosperm	3	0	0	0	0	non-host

197	<i>Prunus mume</i> (Siebold) Siebold & Zucc.		Rosaceae	Angiosperm	12	0	0	0	1	partial
198	<i>Prunus persica</i> (L.) Batsch	Red Haven	Rosaceae	Angiosperm	258	0	44	12	354	partial
199	<i>Prunus sargentii</i> Rehder		Rosaceae	Angiosperm	330	4	17	11	19	host
200	<i>Prunus serrula</i> Franch.	Tibetica	Rosaceae	Angiosperm	36	0	0	0	0	non-host
201	<i>Prunus serrulata</i> Lindl.	Kwanzan	Rosaceae	Angiosperm	504	7	260	24	86	host
202	<i>Prunus serrulata</i> Lindl.	Snowgoose	Rosaceae	Angiosperm	333	1	78	14	58	host
203	<i>Prunus subhirtella</i> Miq.	Autumnalis	Rosaceae	Angiosperm	66	2	74	41	0	partial
204	<i>Prunus subhirtella</i> Miq.	Pendula	Rosaceae	Angiosperm	288	3	29	18	89	host
205	<i>Prunus subhirtella</i> Miq.	Pisnshzam	Rosaceae	Angiosperm	156	2	4	2	15	host
206	<i>Prunus x incam</i>	Okame	Rosaceae	Angiosperm	456	3	169	2	32	host
207	<i>Prunus x yedoensis</i>		Rosaceae	Angiosperm	324	8	175	5	16	host
208	<i>Pseudocydonia sinensis</i> (Dum.Cours.) Koehne		Rosaceae	Angiosperm	96	1	4	12	11	host
209	<i>Pyrus betulifolia</i> Bunge		Rosaceae	Angiosperm	72	1	5	1	8	host

210	<i>Pyrus calleryana</i> Decne.	Cleveland Select	Rosaceae	Angiosperm	132	4	50	57	7	host
211	<i>Pyrus communis</i> L.	Blake's Pride	Rosaceae	Angiosperm	42	0	0	0	11	partial
212	<i>Pyrus communis</i> L.	Sunrise	Rosaceae	Angiosperm	48	0	4	0	14	partial
213	<i>Pyrus fauriei</i> C.K.Schneid.	Westwood	Rosaceae	Angiosperm	48	1	20	0	3	partial
214	<i>Quercus acutissima</i> Carruth.		Fagaceae	Angiosperm	213	3	104	20	7	host
215	<i>Quercus alba</i> L.		Fagaceae	Angiosperm	168	1	56	1	30	host
216	<i>Quercus bicolor</i> Willd.		Fagaceae	Angiosperm	66	0	13	1	1	partial
217	<i>Quercus coccinea</i> Münchh.		Fagaceae	Angiosperm	426	1	50	4	31	host
218	<i>Quercus palustris</i> Münchh.	Green Pillar	Fagaceae	Angiosperm	132	2	19	0	1	partial
219	<i>Quercus robur</i> L.	Fastigiata	Fagaceae	Angiosperm	72	4	26	1	2	host
220	<i>Quercus robur</i> L.	Regal Prince	Fagaceae	Angiosperm	404	12	317	3	49	host
221	<i>Quercus rubra</i> L.		Fagaceae	Angiosperm	726	6	339	4	84	host
222	<i>Rhus typhina</i> L.	Bailtiger	Anacardiaceae	Angiosperm	96	0	0	0	7	partial
223	<i>Sambucus nigra</i> L.	Eva	Adoxaceae	Angiosperm	138	0	0	0	1	partial
224	<i>Sequoiadendron giganteum</i> (Lindl.) J.Buchholz		Cupressaceae	Gymnosperm	3	0	0	0	0	non-host

225	<i>Sophora japonica</i> (L.) Schott	Millstone	Leguminosae	Angiosperm	72	2	201	45	72	host
226	<i>Sophora japonica</i> (L.) Schott	Regent	Leguminosae	Angiosperm	591	10	574	96	305	host
227	<i>Stewartia koreana</i> var.		Theaceae	Angiosperm	157	0	3	0	31	partial
228	<i>Stewartia pseudocamellia</i> Maxim.		Theaceae	Angiosperm	272	2	23	3	67	host
229	<i>Styrax japonicus</i> Siebold & Zucc.		Styracaceae	Angiosperm	642	2	78	15	24	host
230	<i>Styrax obassia</i> Siebold & Zucc.		Styracaceae	Angiosperm	72	0	12	3	2	partial
231	<i>Syringa pekinensis</i> (Rupr.) P.S.Green & M.C.Chang	Morton	Oleaceae	Angiosperm	324	4	96	21	1057	host
232	<i>Syringa pekinensis</i> (Rupr.) P.S.Green & M.C.Chang	Zhang Zhiming	Oleaceae	Angiosperm	117	1	38	24	589	host
233	<i>Syringa reticulata</i> (Blume) H.Hara	Ivory Silk	Oleaceae	Angiosperm	72	1	82	9	7	host
234	<i>Taxus x media</i>	Hatfeldii	Taxaceae	Gymnosperm	12	0	0	0	10	partial
235	<i>Taxus x media</i>	Hicksii	Taxaceae	Gymnosperm	78	0	0	0	2	partial
236	<i>Thuja occidentalis</i> L.	Smaragd	Cupressaceae	Gymnosperm	144	0	9	5	0	partial

237	<i>Thuja plicata</i> Donn ex D.Don	Atrovirens	Cupressaceae	Gymnosperm	105	1	0	0	3	partial
238	<i>Thuja plicata</i> Donn ex D.Don	Emerald Cone	Cupressaceae	Gymnosperm	84	0	0	0	0	non-host
239	<i>Thuja plicata</i> Donn ex D.Don	Zebrina	Cupressaceae	Gymnosperm	78	0	0	0	2	partial
240	<i>Thuja standishii</i> x <i>plicata</i> (Gordon) Carrière	Green Giant	Cupressaceae	Gymnosperm	663	0	22	7	53	partial
241	<i>Tilia americana</i> L.	Redmond	Malvaceae	Angiosperm	132	0	1	3	0	partial
242	<i>Tilia cordata</i> Mill.	Greenspire	Malvaceae	Angiosperm	904	21	365	34	48	host
243	<i>Tilia tomentosa</i> Moench	Sterling	Malvaceae	Angiosperm	495	22	674	38	70	host
244	<i>Tsuga canadensis</i> (L.) Carrière	Pendula	Pinaceae	Gymnosperm	36	0	0	0	0	non-host
245	<i>Ulmus</i>	Patriot	Ulmaceae	Angiosperm	78	1	111	30	6	host
246	<i>Ulmus americana</i> L.	Princeton	Ulmaceae	Angiosperm	564	12	442	38	111	host
247	<i>Ulmus americana</i> L.	Valley Forge	Ulmaceae	Angiosperm	210	11	308	14	100	host
248	<i>Ulmus parvifolia</i> Jacq.	Dynasty	Ulmaceae	Angiosperm	174	0	60	33	3	partial
249	<i>Ulmus parvifolia</i> Jacq.	Emer I	Ulmaceae	Angiosperm	72	0	16	0	4	partial
250	<i>Ulmus parvifolia</i> Jacq.	Emer II	Ulmaceae	Angiosperm	431	2	151	11	35	host

251	<i>Viburnum carlesii</i> Hemsl.	Cayuga	Adoxaceae	Angiosperm	12	0	0	0	1	partial
252	<i>Xanthoceras sorbifolia</i> Bunge		Sapindaceae	Angiosperm	232	0	28	6	17	partial
253	<i>Zelkova serrata</i> (Thunb.) Makino	Green Vase	Ulmaceae	Angiosperm	297	4	32	38	2	host
254	<i>Zelkova serrata</i> (Thunb.) Makino	Village Green	Ulmaceae	Angiosperm	882	15	254	126	18	host

Table 2. List of host ornamental tree and shrub cultivars with highest densities of *Halyomorpha halys*. Density (*H. halys* / tree) was calculated as the total number of *H. halys* nymphs and adults on a cultivar, divided by the multiplicative value of the number of individual trees of a cultivar and the total number of visits to each tree. Twenty five cultivars (~10% of all sampled cultivars) with the highest density are reported here.

Species	Cultivar	Family	Density
<i>Syringa pekinensis</i> (Rupr.) P.S.Green & M.C.Chang	Zhang Zhiming	Oleaceae	5.56
<i>Sophora japonica</i> (L.) Schott	Millstone	Leguminosae	4.42
<i>Syringa pekinensis</i> (Rupr.) P.S.Green & M.C.Chang	Morton	Oleaceae	3.62
<i>Evodia daniellii</i> (Benn.) T.G.Hartley		Rutaceae	3.58
<i>Acer x freemanii</i>	Jeffersred	Sapindaceae	3.30
<i>Acer pensylvanicum</i> L.		Sapindaceae	2.53
<i>Cercis canadensis</i> L.		Leguminosae	2.28
<i>Malus</i>	Mary Potter	Rosaceae	2.18
<i>Ulmus americana</i> L.	Valley Forge	Ulmaceae	2.01
<i>Ficus carica</i> L.	Chicago Hardy	Moraceae	1.93
<i>Acer rubrum</i> L.	Brandywine	Sapindaceae	1.93
<i>Ulmus</i>	Patriot	Ulmaceae	1.88
<i>Acer rubrum</i> L.	Armstrong	Sapindaceae	1.87
<i>Acer rubrum</i> L.	Bowhall	Sapindaceae	1.87
<i>Cladrastis kentukea</i> (Dum.Cours.) Rudd		Leguminosae	1.82
<i>Liquidambar styraciflua</i> L.		Altingiaceae	1.78
<i>Acer rubrum</i> L.	October Glory	Sapindaceae	1.78
<i>Evodia hupehensis</i> (Benn.) T.G.Hartley		Rutaceae	1.76
<i>Malus</i>	Donald Wyman	Rosaceae	1.72
<i>Sophora japonica</i> (L.) Schott	Regent	Leguminosae	1.65
<i>Koelreuteria paniculata</i> Laxm.		Sapindaceae	1.60
<i>Tilia tomentosa</i> Moench	Sterling	Malvaceae	1.58
<i>Cladrastis kentukea</i> (Dum.Cours.) Rudd	Perkins Pink	Leguminosae	1.49
<i>Acer rubrum</i> L.	Franksred	Sapindaceae	1.49

Table 3. List of ornamental tree and shrub ‘non-host’ cultivars with no *H. halys* records.

Species	Cultivar	Family	Classification
<i>Abies nordmanniana</i> (Steven) Spach		Pinaceae	Gymnosperm
<i>Acer davidii</i> Franch.		Sapindaceae	Angiosperm
<i>Acer palmatum</i> Thunb.	Emperor I	Sapindaceae	Angiosperm
<i>Acer palmatum</i> Thunb.	Moonfire	Sapindaceae	Angiosperm
<i>Acer palmatum</i> Thunb.	Sango Kaku	Sapindaceae	Angiosperm
<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Crimson Queen	Sapindaceae	Angiosperm
<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Inaba Shidare	Sapindaceae	Angiosperm
<i>Acer palmatum</i> var. <i>dissectum</i> Thunb.	Seiryu	Sapindaceae	Angiosperm
<i>Aesculus hippocastanum</i> L.	baumannii	Sapindaceae	Angiosperm
<i>Cedrus atlantica</i> (Endl.) Manetti ex Carrière	Kroh's Twisted	Pinaceae	Gymnosperm
<i>Cedrus deodara</i> (Roxb. ex D.Don) G.Don	Karl Fuchs	Pinaceae	Gymnosperm
<i>Cercidiphyllum japonicum</i> Siebold & Zucc. ex J.J.Hoffm. & J.H.Schult.bis	Red Fox	Cercidiphyllaceae	Angiosperm
<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Aurea Nana	Cupressaceae	Gymnosperm
<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Compacta	Cupressaceae	Gymnosperm
<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Gimborn's Beauty	Cupressaceae	Gymnosperm
<i>Chamaecyparis obtusa</i> (Siebold & Zucc.) Endl.	Kosteri	Cupressaceae	Gymnosperm
<i>Cornus kousa</i> F.Buerger ex Hance	Radiant Rose	Cornaceae	Angiosperm
<i>Ginkgo biloba</i> L.	Saratoga	Ginkgoaceae	Gymnosperm
<i>Hamamelis x intermedia</i>	Jelena	Hamamelidaceae	Angiosperm
<i>Hamamelis x intermedia</i>	Pallida	Hamamelidaceae	Angiosperm
<i>Juniperus chinensis</i> L.	Torulosa	Cupressaceae	Gymnosperm
<i>Physocarpus opulifolius</i> (L.) Maxim.	Center Glow	Rosaceae	Angiosperm
<i>Picea breweriana</i> S.Watson		Pinaceae	Gymnosperm
<i>Picea koraiensis</i> Nakai		Pinaceae	Gymnosperm

<i>Picea meyeri</i> Rehder & E.H.Wilson		Pinaceae	Gymnosperm
<i>Picea omorika</i> (Pancic) Purk.	Pendula	Pinaceae	Gymnosperm
<i>Picea pungens</i> Engelm.	Fastigiata	Pinaceae	Gymnosperm
<i>Picea pungens</i> Engelm.	Glauca	Pinaceae	Gymnosperm
<i>Picea pungens</i> Engelm.	Glauca Iseli Fastigata	Pinaceae	Gymnosperm
<i>Picea pungens</i> Engelm.	Glauca Majestic Blue	Pinaceae	Gymnosperm
<i>Picea pungens</i> Engelm.	Hoopsii	Pinaceae	Gymnosperm
<i>Pinus cembra</i> L.	Chalet	Pinaceae	Gymnosperm
<i>Pinus densiflora</i> Siebold & Zucc.	Umbraculifera	Pinaceae	Gymnosperm
<i>Pinus koraiensis</i> Siebold & Zucc.		Pinaceae	Gymnosperm
<i>Pinus nigra</i> J.F.Arnold	Arnold Sentinel	Pinaceae	Gymnosperm
<i>Pinus parvifolia</i>		Pinaceae	Gymnosperm
<i>Pinus strobus</i> L.	Pendula	Pinaceae	Gymnosperm
<i>Pinus thunbergii</i> Parl.	Thunderhead	Pinaceae	Gymnosperm
<i>Prunus mume</i> (Siebold) Siebold & Zucc.	Bonita	Rosaceae	Angiosperm
<i>Prunus serrula</i> Franch.	Tibetica	Rosaceae	Angiosperm
<i>Sequoiadendron giganteum</i> (Lindl.) J.Buchholz		Cupressaceae	Gymnosperm
<i>Thuja plicata</i> Donn ex D.Don	Emerald Cone	Cupressaceae	Gymnosperm
<i>Tsuga canadensis</i> (L.) Carrière	Pendula	Pinaceae	Gymnosperm

Figure 1. Venn diagram representing the number of cultivars of ornamental trees and shrubs used by different life stages of *Halyomorpha halys*. The size of a circle represents the number of cultivars on which the stink bugs were recorded. Green boarder = adults, Blue boarder = nymphs, Red boarder = eggs. Colors represent distinct host use and overlapping host use. For example, lilac means nymphs had 11 distinct hosts and orange means that nymphs and adults shared 72 hosts.

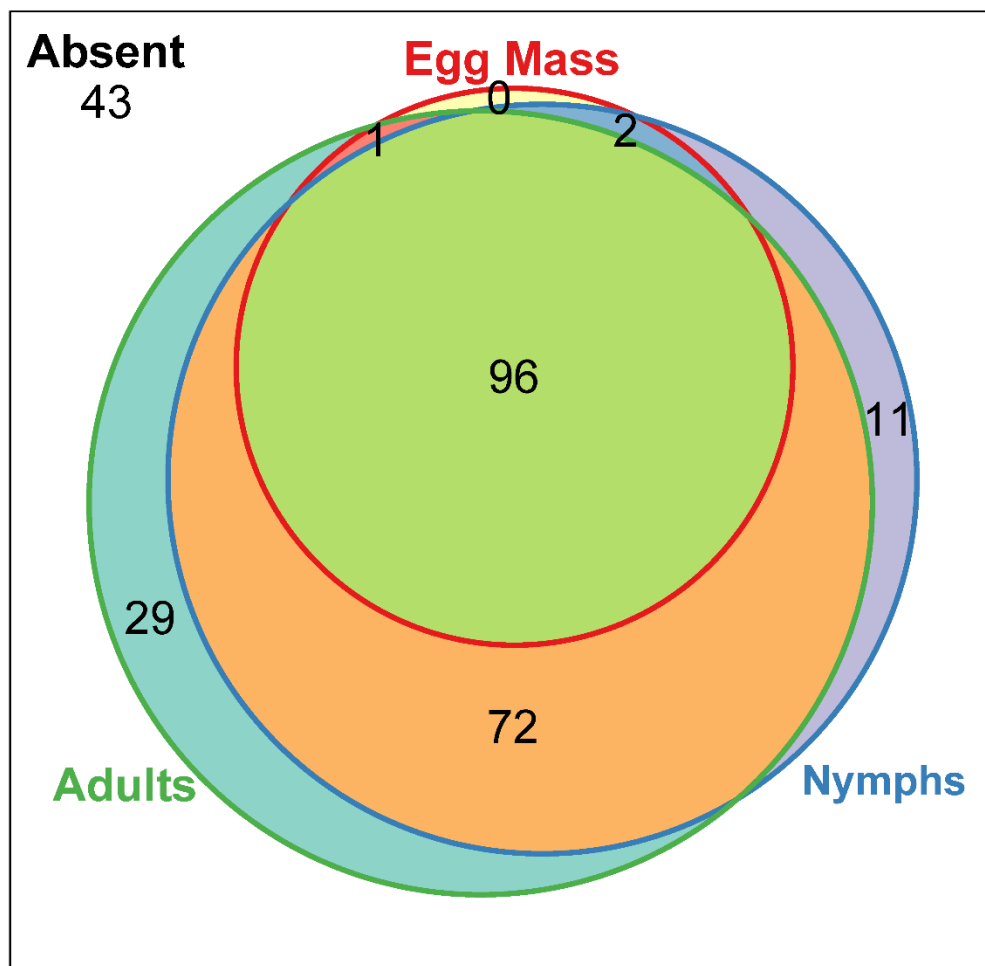
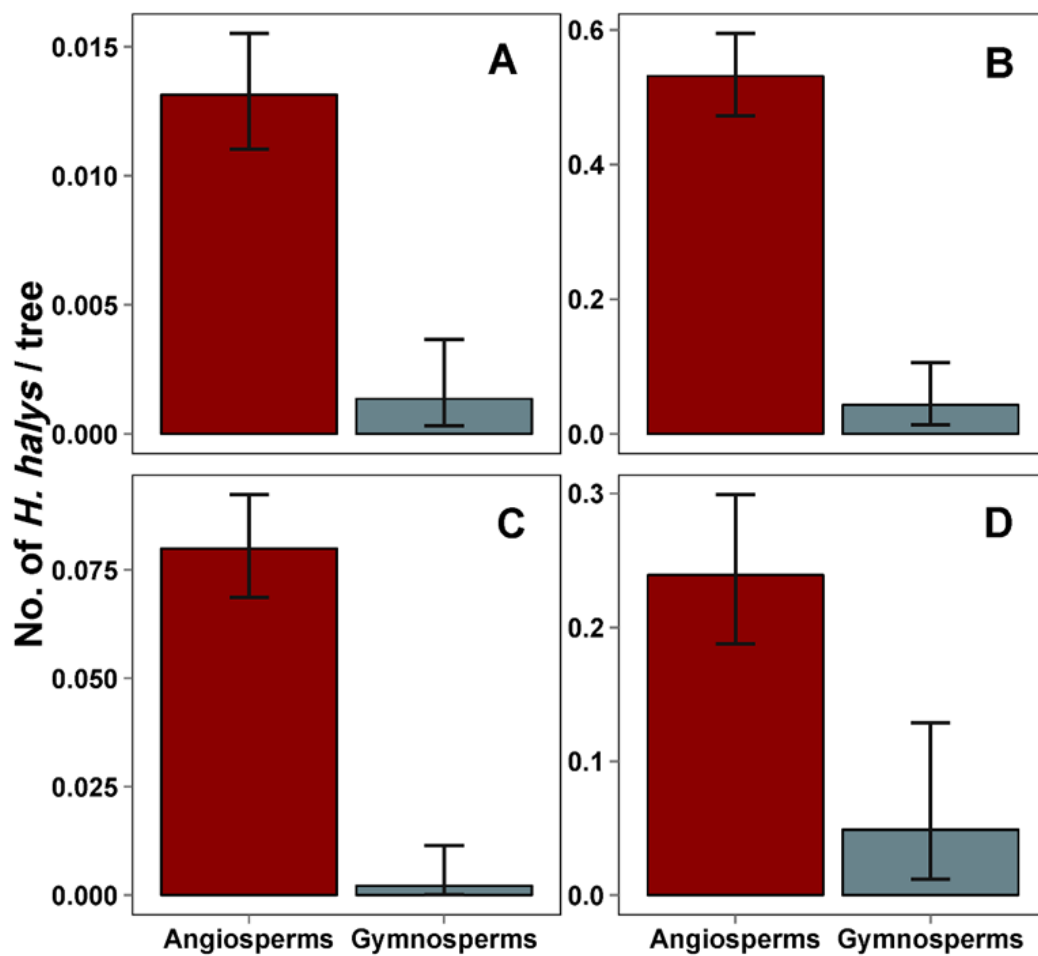


Figure 2. Relationship between *Halyomorpha halys* abundance and taxonomic status of the cultivars of ornamental trees and shrubs across the stink bug life stages estimated through GLMs. Model estimated mean abundances (and 95 % CI) are plotted for A) egg masses, B) early nymphs, C) late nymphs and D) adults. For each life stage angiosperms housed significantly more *H. halys* than gymnosperms based on Tukey's HSD comparisons ($\alpha = 0.05$).



Chapter 2: Influence of host origin on patterns of host use by brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae).

Abstract

In this chapter I explore the influence of geographic origin on *H. halys* use of the 254 woody ornamental plant cultivars surveyed at commercial nurseries in Maryland during 2011-2013. Further analysis of this generalist pentatomid offers further insight into patterns of host use by invasive insects. Overall, I found *H. halys* were less abundant than Asian cultivars than non-Asian cultivars. However, the strongest trends identified were in the genera *Acer*, *Ulmis*, and *Pyrus* where *H. halys* was more abundant on naïve non-Asian cultivars than Asian cultivars. These results lend support to Gandhi and Herms' defense free space hypothesis and are consistent with patterns of herbivory recorded in other invasive insect introductions. The influence of fruit on *H. halys* host selection and its implications for the design of landscapes refractory to *H. halys* are also discussed.

Introduction

The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) is native to Japan, China, Taiwan, and Korea. It was first discovered in the United States near Allentown, PA in the middle 1990's (Hoebeke and Carter 2003). To date *H. halys* has been reported in 42 states, the District of Columbia, and two Canadian provinces in North America (Northeast IPM Center 2015). In Europe *H. halys* has invaded Lichtenstein and Switzerland (Wermelinger et al. 2008), France

(Callot and Brua 2013), Italy (Pansa et al. 2013), Germany (Heckmann 2012), and Hungary (Vetek et al. 2014).

Several authors have detailed the highly polyphagous nature of *H. halys* in its native and invaded ranges. An important review of the Asian literature by Lee et al. (2013) revealed 106 hosts distributed in 45 families ranging from herbaceous annual vegetable crops to forest trees. Lee et al. (2013) noted a preponderance of hosts in the Fabaceae and Rosaceae in Asia. In North America, studies conducted by Bernon (2004) in several counties in eastern Pennsylvania reported *H. halys* on 73 species of plants ranging from annual crops to landscape trees. Trees and shrubs, many of which were non-native to North America, dominated the list of plants upon which *H. halys* was noted as abundant or common (Bernon 2004). A quantitative survey of 13 ornamental and cultivated hosts used by *H. halys* nymphs and adults confirmed that at certain times of the season, in addition to Asian hosts, North American hosts such as American ash supported high numbers of *H. halys* (Nielsen and Hamilton 2009). A recent report by Bakken et al. (2015) revealed the greatest numbers of *H. halys* on tree of heaven, catalpa, yellowwood, paulownia, cherry, walnut, and redbud growing in non-managed woodlands in North Carolina and thereby confirming the use of both Asian and non-Asian hosts in the North American invaded range. In Europe a synthesis by Haye et al. (2014) reported 51 host plants in 32 plant families. This list included European natives and non-native plants ranging from herbaceous perennials to woody trees and shrubs. Among species with the highest observed densities, no clear pattern emerged with respect to plant provenance (Haye et al. 2014).

In a previous study, I linked the presence of fruits to elevated abundance of *H. halys* on different species and cultivars of plants in commercial nurseries (Martinson et al. 2015). In Chapter 1 of this thesis, I identified several cultivars of woody landscape plants not used by any life stage of *H. halys* and discussed their importance as components of landscapes refractory to populations of *H. halys*. Chapter 1 also revealed a strong pattern of preferential use of angiosperms compared to gymnosperms by all life stages of *H. halys*. Within the realm of invasion ecology several hypotheses seek to explain the interactions between plants and non-native arthropods in the invaded range. In a series of studies, Tallamy and colleagues (Tallamy 2004, Tallamy and Shropshire 2009, Burghardt et al. 2009, Tallamy et al. 2009, and Burghardt et al. 2010) found non-native plants supported fewer species, less biomass, and lower abundances of Lepidoptera than native plant species. These results were attributed to the inability of many native insects to recognize non-native plants as hosts due to their coevolutionary history with native plants and a lack thereof with non-native plants. In an interesting contrast, Gandhi and Herms (2010) suggested in their “defense free space” hypothesis that native plants may lack coevolved defenses against herbivores from outside their native range. They argued that once these aliens arrive they enter and thrive in defense free space, and plants with which herbivores share a coevolutionary history are defended and suffer less herbivory than naïve plants. Evidence supporting defense free space is found in several insects lacking a long shared coevolutionary history with their host plants including specialists like emerald ash borer (Rebek et al. 2008, Martinson et al. 2014), bronze birch borer (Nielsen et al. 2011), viburnum leaf beetle (Desurmont et

al. 2011), and hemlock woolly adelgid (McClure 1992, 1995, Montgomery et al. 2009).

The use of resistant plant material is a mainstay of integrated pest management for agronomic crops (Painter 1951, Maxwell and Jennings 1980) as well as ornamental plants in landscapes (Potter 1986, Raupp et al. 1992, Herms 2002). Several of the studies mentioned previously (Bernon 2004, Nielsen and Hamilton 2009, Bakken et al. 2015) noted the predilection of *H. halys* for trees of Asian origin. By contrast Haye et al. (2014) found no distinct pattern of host associations based on provenance for *H. halys* in Europe. The primary goal of this study was to assess use of ornamental woody plants from different realms, those in which *H. halys* shared an evolutionary history with its hosts, explicitly Asia, compared to those in newly invaded realms including Europe and North America. All plants in this study were grown in commercial nurseries for future use in landscaping. My hope is that plant origin may be useful in assessing whether or not a plant will be used by *H. halys*. By incorporating resistant plants into landscapes, breeding sites and places where stink bugs aggregate prior to entering homes could be eliminated. This should reduce the need for treating plants with insecticides to kill this pest in landscapes (Cooper 2010). Moreover, by identifying ornamental plants refractory to this pest, commercial growers of landscape plants could enjoy a marketing advantage by producing and selling plants that reduce the likelihood of autumnal home invasions.

Materials and Methods

Field Site Description, Tree Selection and Identification

During a 3 year period through the spring, summer, and autumn of 2011 - 2013 *H. halys* was sampled in two commercial woody plant nurseries located in Frederick and Montgomery Counties, MD. Timed visual surveys of *H. halys* life stages were recorded in each nursery on trees and shrubs on multiple occasions each year. Surveys conducted in 2011 occurred at several production fields at Raemelon Farm in Adamstown in western MD (39.299813 latitude; 77.478700 longitude) and in 2012 and 2013, surveys were conducted at several production fields at Raemelon Farm and Ruppert Nurseries in Laytonsville in central MD (39.212633; 77.142759). Production fields at Ruppert Nurseries consisted of 20 rows of 25–35 ornamental trees and shrubs. Raemelon fields were larger and consisted of 80–150 rows of 25-35 ornamental plants. Rows at both locations were spaced approximately 3 m apart and depending on the size of the plant, plants within rows were approximately 2 m apart. Plants ranged in height from 1 to 4 m. Six trees of each cultivar were surveyed in each row. These nurseries were planted with a wide variety of trees. Specifically, single cultivars were typically planted within a row, but fields differed in cultivar composition. Following the protocols of Venugopal et al. (2015) and Martinson et al. (2015) 1-min visual counts of *H. halys* were conducted on foliage, flowers, fruits/seeds, and bark to a height of up to 3 m. Undergraduate and graduate student observers were trained by myself and Dr. Michael Raupp to ensure uniformity and consistency in the field protocols for data collection. *H. halys* abundance was recorded separately for four life stages: egg masses, early instar nymphs (instars 1 –

3), late instar nymphs (instars 4 and 5), and adults. Each year, repeated counts were conducted at each tree in early June, late June, mid-July, and early August. Some sampled trees were sold during the study period; tree mortality from heat stress, disease, and physical damage also resulted in variable numbers of readings or ‘tree visits’ for some trees. Within these two nurseries we surveyed 123 woody ornamental tree cultivars of 11 genera with both Asian and non-Asian representatives for the presence of *H. halys*. Of the 11 genera, five genera of gymnosperms (17 Asian cultivars and 27 non-Asian cultivars) were surveyed including *Abies* Mill. (Fir), *Cedrus* Trew (Cedar), *Chamaecyparis* Spach (False Cypress), *Picea* A. Dietr. (Spruce), and *Pinus* L. (Pine). The six genera of angiosperms (41 Asian cultivars and 38 non-Asian cultivars; Table 4) included *Acer* L. (Maple), *Cornus* L. (Dogwood), *Prunus* L. (Cherry), *Pyrus* L. (Pear), *Quercus* L. (Oak), and *Ulmus* L. (Elm) (Table 4). By including both Asian and non-Asian cultivars for each genus, we controlled in part for the phylogeny and shared evolutionary history of cultivars while comparing them for their influence on *H. halys* abundance. Tree genus, species, and cultivar, if applicable, were recorded. Identification was completed using nursery records and confirmed using existing literature (Dirr 2009, The Plant List 2013) to ensure consistent usage of cultivar names, common names, and spellings.

Statistical analyses

Data on the abundance of each stink bug life stages on each ornamental tree cultivar was pooled over years and site for further analysis. The influence of tree origin on *H. halys* was analysed through generalized linear mixed effects models (GLMM) assuming a Poisson error distribution and log link function (Bolker et al.

2009). Separate GLMMs were performed for angiosperms and gymnosperms. GLMMs were performed for each life stage with the abundance of *H. halys* as the response variable, origin as the predictor, and tree cultivar as a random effect, while offsetting differences in tree visits across the cultivars. Similarly, GLMM analyses testing the influence of tree origin for each of the Angiosperm genera was also performed for each life stage. The significance of the fixed effects was determined by Wald χ^2 tests and in cases with significant fixed effect, significant differences in the model estimated means were identified through Tukey's HSD comparisons ($\alpha = 0.05$).

All statistical analyses were performed in R program (R Development Core Team 2014) and associated statistical packages. GLMMs were performed with package lme4 (Bates et al. 2013), Tukey's HSD comparisons of means were computed with package 'multcomp' (Hothorn et al. 2008), and GLMMs estimated coefficients were plotted using 'ggplot2' (Wickham 2009).

Results

For angiosperms, *H. halys* abundance was significantly influenced by host origin for all life stages except late instar nymphs (egg masses - $\chi^2 = 4.9$, $df = 1$; $P = 0.028$; early nymphs - $\chi^2 = 12.4$, $df = 1$; $P < 0.001$; late nymphs - $\chi^2 = 1.6$, $df = 1$; $P = 0.20$; adults - $\chi^2 = 179785$, $df = 1$; $P < 0.001$) (Fig. 1). Non-Asian tree cultivars harbored significantly higher numbers of egg masses, early nymphs and adults (Tukey's HSD, $P < 0.05$; Figure 3) than Asian cultivars. *H. halys* abundance on non-Asian tree cultivars was 2, 4.3, and 2.4 times higher for egg masses, early nymphs, and adults respectively, than tree cultivars of Asian origin. The significant differences

between Asian and non-Asian cultivars were primarily driven by the abundance of *H. halys* observed in cultivars of *Acer*, *Ulmus*, and *Pyrus* (Table 5, Fig.1, Fig. 2).

Egg masses were not recorded on gymnosperms. GLMM analysis showed that gymnosperm cultivar origin did not significantly influence the abundance of all the *H. halys* other life stages (early nymphs - $\chi^2 = 0.006$, $df = 1$; $P = 0.93$; late nymphs - $\chi^2 = 0.001$, $df = 1$; $P = 0.97$; and adults - $\chi^2 = 1.5$, $df = 1$; $P = 0.22$) and hence Tukey's comparison were not performed. The raw means for observed *H. halys* abundance for each of the genera and life stages for both angiosperms and gymnosperms is provided in Table 5. GLMM analysis showed consistently significant differences between non-Asian and Asian cultivars for these three genera across life stages (Fig. 2).

Discussion

In general cultivars not from Asia housed more *H. halys* than those from Asia although much variation was observed among genera. The strongest associations were seen in *Acer*, *Ulmus*, and *Pyrus* where one or more life stages of *H. halys* were more abundant on non-Asian compared to Asian cultivars (Fig. 2). *Prunus* was an exception in the case of egg masses as *H. halys* preferred Asian cultivars as oviposition sites. Overall these results lend support for the defense free space hypothesis (Gandhi and Herms 2010) and are consistent with those of other researchers who have found naïve hosts, those lacking a coevolutionary history with a pest, to support greater numbers of herbivores or levels of herbivory following arrival of an exotic pest in a newly invaded range (McClure 1992, 1995, Rebek et al. 2008, Montgomery et al. 2009, Desurmont et al. 2011, Nielsen et al. 2011, Martinson et al.

2014). This is the first documented case of a generalist pentatomid conforming to the predictions of the defense free space hypothesis.

My previous studies demonstrate the importance of fruit in fostering elevated numbers of *H. halys* on woody landscape plants (Martinson et al. 2015). These results support earlier work by Martinson et al. (2013) indicating the strong preference of *H. halys* for carbohydrate rich plant tissues. In Chapter 1, I demonstrate the preference of angiosperms relative to gymnosperms used by this highly invasive pest. In this study, I demonstrate an increased risk to native North American hosts particularly in the genera *Acer*, *Ulmus*, and *Pyrus*. Raupp et al. (2006) previously identified *Acer* and *Ulmus* as genera at risk to other invasive non-native insect pests. In sum, these findings refine our ability to select landscape plants for those attempting to design landscapes refractory to *H. halys*. Landscapes comprised of gymnosperms will be support far fewer *H. halys* than those with angiosperms. Fruitless varieties or varieties that fruit when *H. halys* is not active will support fewer *H. halys* than varieties with fruit (Martinson et al. 2015). If landscape architects and property owners desire landscapes refractory to *H. halys* comprised of *Acer*, *Ulmus*, and *Pyrus*, then Asian cultivars may provide advantage over North American cultivars. Finally, growers of woody landscape plants may enjoy a marketing advantage by producing and marketing genera and cultivars of plants that do not support *H. halys* in the invaded range of this pest.

Table 4. List of genera and number of ornamental tree cultivars of Asian and non-Asian origin surveyed for *Halyomorpha halys*.

classification	genus	Asian	non-Asian	Total
Angiosperms	<i>Acer</i>	14	12	26
	<i>Cornus</i>	8	8	16
	<i>Prunus</i>	12	7	19
	<i>Pyrus</i>	3	2	5
	<i>Quercus</i>	1	7	8
	<i>Ulmus</i>	3	2	5
Gymnosperms	<i>Abies</i>	1	2	3
	<i>Cedrus</i>	2	2	4
	<i>Chamaecyparis</i>	5	2	7
	<i>Picea</i>	2	16	18
	<i>Pinus</i>	7	5	12
Total		58	65	123

Table 5. Mean abundance (\pm SE) of *Halyomorpha halys* life stages recorded in tree cultivars of 11 Genera, with both Asian and non-Asian origin.

Taxonomy	Genus	Asian				Non-Asian			
		Egg mass	Early Nymphs	Late Nymphs	Adults	Egg mass	Early Nymphs	Late Nymphs	Adults
Angiosperms	<i>Acer</i>	0.001 \pm 0.001	0.119 \pm 0.07	0.004 \pm 0.003	0.025 \pm 0.012	0.022 \pm 0.003	1.361 \pm 0.18	0.184 \pm 0.04	0.144 \pm 0.05
	<i>Cornus</i>	0.003 \pm 0.003	0.128 \pm 0.07	0.033 \pm 0.014	0.124 \pm 0.04	0.000	0.158 \pm 0.04	0.005 \pm 0.004	0.193 \pm 0.08
	<i>Prunus</i>	0.009 \pm 0.003	0.261 \pm 0.10	0.074 \pm 0.05	0.199 \pm 0.11	0.002 \pm 0.001	0.168 \pm 0.82	0.034 \pm 0.013	0.323 \pm 0.07
	<i>Pyrus</i>	0.022 \pm 0.005	0.288 \pm 0.11	0.149 \pm 0.15	0.076 \pm 0.02	0.000	0.042 \pm 0.04	0.000	0.277 \pm 0.02
	<i>Quercus</i>	0.014	0.488	0.094	0.033	0.017 \pm 0.007	0.343 \pm 0.09	0.008 \pm 0.002	0.077 \pm 0.02
	<i>Ulmus</i>	0.002 \pm 0.002	0.306 \pm 0.04	0.072 \pm 0.06	0.051 \pm 0.02	0.037 \pm	1.125 \pm 0.34	0.067 \pm 0.003	0.336 \pm 0.14
Gymnosperms	<i>Abies</i>	0.000	0.005	0.000	0.013	0.000	0.000	0.000	0.056 \pm 0.056
	<i>Cedrus</i>	0.000	0.021 \pm 0.021	0.000	0.031 \pm 0.031	0.000	0.000	0.000	0.004 \pm 0.004
	<i>Chamaecyparis</i>	0.000	0.000	0.000	0.001 \pm 0.001	0.000	0.008 \pm	0.000	0.030 \pm 0.030
	<i>Picea</i>	0.000	0.000	0.000	0.000	0.000	0.005 \pm	0.000	0.032 \pm 0.023
	<i>Pinus</i>	0.000	0.001 \pm 0.001	0.000	0.014 \pm 0.012	0.000	0.137 \pm 0.137	0.004 \pm 0.004	0.160 \pm 0.14

Figure 3. Relationship between *Halyomorpha halys* abundance and origin of the angiosperm cultivars of ornamental trees and shrubs across the stink bug life stages. GLMM estimated mean abundances (and 95 % CI) are plotted for A) egg masses, B) early nymphs (2nd & 3rd instars), C) late nymphs (4th & 5th instars), and D) adults. Significant differences in mean values based on Tukey's HSD comparisons are indicated by different letters above bars ($\alpha = 0.05$).

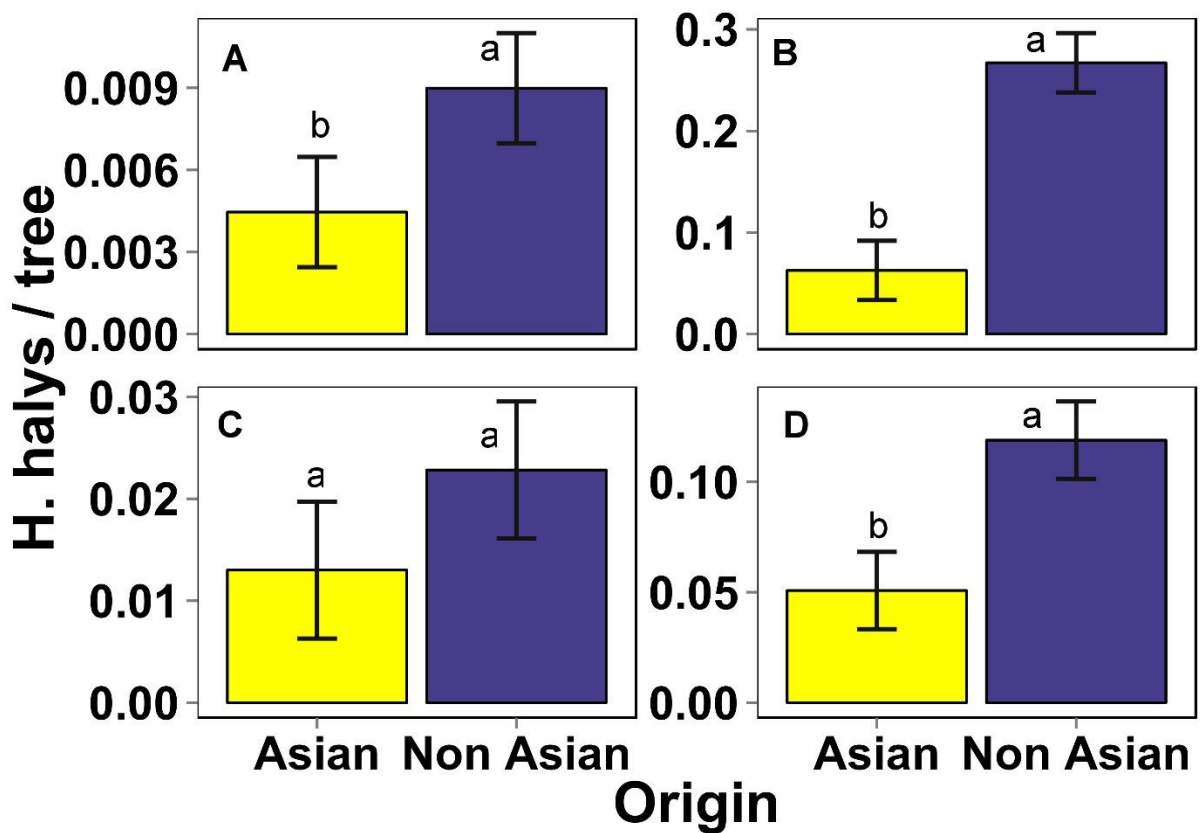
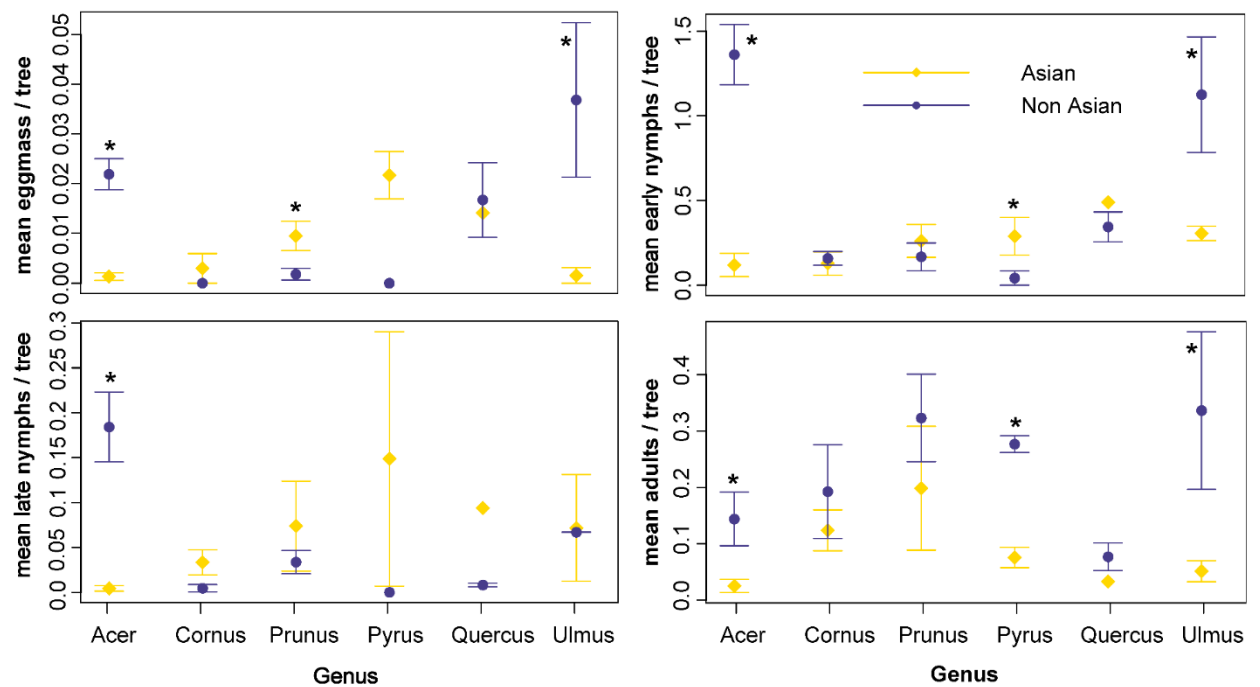


Figure 4. Mean abundance (\pm SE) of *Halyomorpha halys* life stages recorded in tree cultivars of 11 Genera, with both Asian and Non-Asian origin. For each life stage, significant difference between non-Asian and Asian for each of the Genera, based on GLMM and Tukey's comparison, is denoted by an asterisk.



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